

## Spring migration routes and timing of Greenland white-fronted geese – results from satellite telemetry

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Greenland white-fronted geese accumulate body mass throughout late winter in preparation for migration after mid-April to spring staging areas in Iceland. This analysis presents field assessment of abdominal fat deposits (API) from large samples of marked birds which showed increasing rates of fuel deposition throughout January–April. Historical records show that geese rarely depart en masse before 17 April, a pattern followed by all but one of the tagged birds. Timed positions obtained from 12 geese fitted with satellite transmitters in 1997, 1998 and 1999 suggested that all geese departed winter quarters on tailwinds between 16 and 19 April. Tracked geese flew directly to staging areas in Iceland, although one staged for 10 days in Northern Ireland in 1997 and another may have stopped briefly in western Scotland. Average migration duration of all tagged birds departing Ireland (including the 1997 bird that stopped over within Ireland) was 25 hours (range 13–77). Four geese apparently overshot and returned to Iceland during strong E to ESE winds. APIs in Iceland showed more rapid and linear increases in stores during the mean 19-day (range 13–22) staging period there than on the winter quarters. Geese continued their migration to Greenland when APIs attained or exceeded levels at departure from Ireland and all departed on assisting tailwinds between 1 and 11 May. Tracked birds continued the journey to West Greenland in between 24 and 261 (mean 82) hours, although one bird turned back during the traverse of the Greenland Ice Cap and summered on the east coast. Seven of the birds staged for 1–20 hours at, or near, the East Greenland coast and several made slow progress crossing the inland ice, all in the direction of their ultimate destination (i.e. not necessarily taking the lowest or shortest crossing routes). It is suggested that the energy-savings of departing on tailwinds may favour geese to wait for such conditions once threshold fat storage levels have been reached, but more research is needed to confirm this.

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Greenland white-fronted geese *Anser albifrons flavirostris* breed in West Greenland and migrate through Iceland to winter in Britain and Ireland. After population declines from the 1950s to the 1970s, under protective legislation on the wintering grounds the population doubled to a level of 30–35,000 (Ruttledge and Ogilvie 1979, Fox et al. 1998a). In very recent years, numbers have fluctuated and, as a result of reductions in repro-

ductive success, now show signs of decline (Fox 2002). Declines and extinctions at some wintering resorts continue, despite the conservation objective of maintaining the current geographical range of the population. To provide appropriate nature conservation management strategies to safeguard the population, we need to understand factors limiting population size and regulating its rate of change. Research attention has focussed

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on establishing those periods and events in the annual cycle, which may be critical in terms of limiting survival and reproductive output.

Foremost amongst these events are spring migration and the prelude to nesting. Greenland white-fronted geese fly 1500 km from Ireland and Britain to Iceland, where they stage between ca 10 April and ca 12 May to recoup depleted stores (Francis and Fox 1987, Fox et al. 1999, Nyegaard 2001). They then fly 1500 km across the ocean and cross the 2500 m high Greenland Ice Cap, initially to spring staging areas before local movements within Greenland to ultimate summering areas along the west coast (Glahder 1999a, b, Glahder et al. 1999, 2002). Successful completion of both migratory legs of this journey necessitates acquisition of sufficient stored energy to fuel flight costs and to provide some insurance against the costs of arrival to unfavourable feeding conditions. Potentially, those individuals arriving earliest on breeding areas in best condition (i.e. with unexploited energy stores) will also gain advantage in terms of reproductive investment (Ebbinge and Spaans 1995). Geese presumably trade off the costs and risks involved in carrying extra mass (e.g. the enhanced energetic costs of carrying extra fuel or potential mass-dependent predation risk) against risks of exhaustion of body stores and reserves before completion of the journey (McNamara and Houston 1990, Witter and Cuthill 1993, Bednekoff and Houston 1994). Hence, migratory geese are likely to show adaptations that minimise their energy expenditure en route to the breeding grounds in spring, such as selecting appropriate weather conditions for migration (Green et al. 2002). However, to wait for assisting tailwinds, for example, may potentially involve loss of condition (Prop et al. 2003), delay arrival and reduce the potential for reproductive investment. Although the overall pattern and timing of spring migration in this population is well described, information on how individuals conduct migration is lacking. In this paper, we report the results from a satellite telemetry study to describe the timing of migration of, and the routes taken by, individually tagged Greenland white-fronted geese. The results are presented in the context of observations of general patterns of fat deposition sampled amongst large samples of birds over a number of years throughout the entire spring migration.

## Methods

### Satellite telemetry

The study was centred on Wexford North Slob, south-east Ireland (52° 22'N 6° 24'W), where 6,000–10,000 birds have wintered recently (Fox et al. 1998a). After attachment trials with short-range VHF radios (Glahder et al. 1997), geese were cannon-netted over bait and a sample of adult male individuals fitted (using

knicker elastic harnesses) with PTT100 satellite transmitters (Microwave Technology Inc.). Adult males were selected to avoid potential effects on female breeding performance (Ward and Flint 1995). In 1997, seven 20 g PTTs were attached but six of these failed one to three days after attachment (probably due to antenna mounting weakness). Thirty gram transmitters were used in 1998 (on 6 individuals) and 1999 (8 individuals) fitted with 2 mm braided wire antennae (as compared to 1 mm in 1997) and protected at the base with a 4 cm spring (absent from 20 g versions) to avoid damage by geese (Glahder et al. 1999). Each bird was marked with orange neck collar and white leg ring engraved with a three-symbol code to enable recognition in the field (Glahder et al. 1999, 2002). PTTs were programmed to transmit for 8 hours before “resting” for 29 hours, sending signals containing data on temperature, battery voltage and goose activity every 90 seconds (1997 and 1998) and 60 seconds (1999) during the on-cycle. Transmissions were received by polar orbiting NOAA satellites, downloaded by Argos CLS in Toulouse France who supplied data on-line. Timed positions (UTC) were calculated by Argos using their standard algorithms and on this basis assigned to accuracy classes as follows. High quality positions were generated on the basis of at least four signals being received during a satellite pass over the transmitter, defined as class 3 (< 150 m), 2 (150–350 m), 1 (350–1000 m) or 0 (> 1 km). Class A and B positions were based on three or two signals respectively and these locations could not be assigned to distance accuracy (ARGOS CLS 1996). On the basis of these positions, distances and directions were calculated using standard algorithms for loxodromes (Imboden and Imboden 1972). Departure and arrival times from staging areas in Ireland and Iceland, and to staging areas in Ireland, Iceland and Greenland, were defined in three ways with decreasing accuracy. The best defined times were back- or forward calculated from two or more positions obtained during migration using the actual ground speed of the goose. If only one position was available during a migration flight, ground speed was considered to be 60 km h<sup>-1</sup>. Poorest quality departure/arrival times consisted of only last and first up links received from staging areas, when earliest and latest departure/arrival times were calculated on the basis of a ground speed of 60 km h<sup>-1</sup>.

### Body condition during the prelude to departure, Wexford

Between 29 and 164 Greenland white-fronted geese were caught annually using cannon-nets at Wexford every year from 1983–2000, resulting in a total sample of 1370 individuals. Each bird was sexed (by cloacal examination) and aged (by plumage characteristics,

Owen 1980). Most were released bearing an engraved neck collar with a unique letter/digit combination repeated on a leg ring, enabling subsequent recognition in the field (Wilson et al. 1991). AJW undertook field determinations of the abdominal profiles indices (API) of these collared birds in the field 12–16 days per month, using techniques described by Owen (1981) modified according to Boyd et al. (1998). This score reflects the extent of fat store deposits in the abdomen, the site of the most important fat store in migratory geese (Thomas et al. 1983) and a linear relationship between body mass and API has been demonstrated in this and other species (J. Madsen, unpubl., Fox et al. 1998b, Nyegaard 2001, Fox 2002, but see Fig. 1 below).

### Ground wind conditions at departure from Ireland

For the three springs considered in depth here, we used the reserve log books from the Wexford Wildfowl Reserve to determine the days when there were the largest departures of geese from the site. The Irish Meteorological Office station at Kilkenny, 52° 39' N 7°15' W (66 km WNW of Wexford) supplied mean hourly ground level wind strength (in  $\text{m s}^{-1}$ , based on sixty minute interval measurements) and direction (degrees from north), the only wind material available for the years 1997–1999. For each mean value, the wind effect (calculated ground speed minus assumed air-

speed) was calculated based on the expected head- or tailwind vectors under the prevailing conditions, assuming an airspeed for the geese of  $60 \text{ km h}^{-1}$  (Piersma and Jukema 1990).

### Body condition prior to departure from Iceland to Greenland

Daily counts and observations of marked geese were undertaken at Hvanneyri Agricultural College in western Iceland (64° 34'N 21° 46'W) during 17 April–9 May 1997, 18 April–7 May 1998 and 15 April–10 May 1999. Abdominal profiles scores were compiled daily by skilled observers, although no data are presented for days with sample sizes less than 20 observations. In 1999, 66 White-fronted geese were caught at the farm during 6 cannon-net catches on different dates. All were aged, sexed and measured according to the procedure at Wexford, an assessment of abdominal profile made during processing (Fox et al. 1998b, Nyegaard 2001) and released with collars and leg bands.

### Departure times of satellite versus all birds in Iceland

At least three counts of the Hvanneyri farm were carried out each day during the staging period, enabling

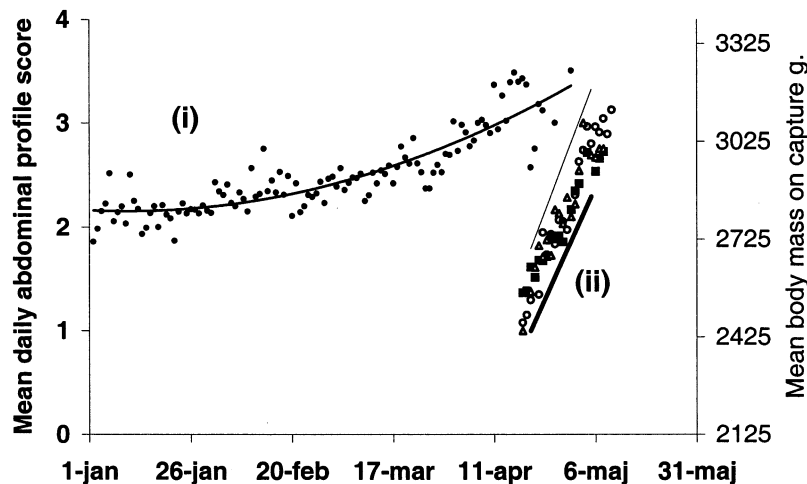


Fig. 1. (i) Mean daily abdominal profile scores of Greenland white-fronted geese sampled in the field at Wexford Slobs during 1983/84–1999/2000 inclusive, showing best fit second-order polynomial regression (to left in figure). Regression model of mean abdominal profile score (API in standard units) and date ( $t$  in days after 1 January) was  $\text{API} = 9.96 \times 10^{-5}t^2 - 1.80 \times 10^{-3}t + 2.161$ . The relatively low values of 19 and 20 April were due to very small sample sizes on these days ( $n = 7$  and  $n = 2$ , respectively). (ii) Mean daily abdominal profile scores of Greenland white-fronted geese during spring staging from Hvanneyri, western Iceland (to right of figure). Symbols indicate mean API values from birds not assigned to sex class in 1997 (solid squares), 1998 (open triangles) and 1999 (open circles). For comparison, the thin solid line represents the regression of male body mass (rate of increase  $32.6 \text{ g day}^{-1}$ ,  $F_{1,25} = 7.5$ ,  $P = 0.012$ ) and thick solid line that of female body mass (rate of increase  $27.6 \text{ g day}^{-1}$ ,  $F_{1,37} = 13.5$ ,  $P < 0.001$ ) on dates from 6 catch events throughout the staging period in 1999, plotted on the right hand axis. Individual values are omitted for clarity, for full details see Nyegaard (2001) and Fox (2002).

some assessment of the numbers present and the period over which the last 50% of the maximum numbers present departed (see Fig. 4 in Fox et al. 1999).

### Ground wind conditions at departure

Ground level wind strength (in  $\text{m s}^{-1}$ ) and direction (degrees from north) at 3 hour intervals from 09:00 am to 09:00 pm were obtained from the Icelandic Meteorological Office station at Stafholtsey,  $64^{\circ} 37' \text{ N } 21^{\circ} 36' \text{ W}$ , 10 km NE of Hvanneyri. For each value, the degree of assistance flying geese would gain was calculated in the same way as for Wexford.

## Results

### Body condition during the prelude to departure, Wexford

Fitted regression models to individual weight (combined from captures in all years combined) regressed on date shows a polynomial relationship between body mass and date for all age and sex classes (Fox 2002). These patterns represent a slight decline in mass from arrival until December followed by an increasing rate of accumulation until the latest catches on 4 April. This pattern corresponds well with that obtained from the mean daily API score for all years combined, for which data are available through until final departure (Fig. 1). The fall in mean values after 18 April is based on very small sample sizes, drawn from individuals remaining after the departures of the majority of marked individuals.

### Departure times of birds at Wexford

Although some departures of geese from Wexford take place in the first half of April, based on the resightings of marked birds during 1984–2000, there was rarely a mass departure before 17 April, after which, the probability of resighting marked birds falls markedly (unpublished data). Departure times of transmitter tagged birds are shown in Fig. 2 and 3. The reserve logs indicated that large numbers departed Wexford on 7–8 April 1997, 16–18 April 1997, 16–18 April 1998 and (16)–18–19 April 1999, coinciding with movement of birds fitted with PTTs (Fig. 3).

In 1997, when only one satellite transmitter continued to function for the duration of the migration episode to Iceland, that bird left Wexford early morning on 7 April and moved to a staging area in Lough Foyle, Northern Ireland, where it remained until 16 April. In all cases (including the movement within Ireland in 1997), the last up-link from geese departing Wexford predated favourable tailwinds (Fig. 3), although samples sizes were too small to test this statistically. Although geese seemingly did not depart for Iceland on tailwinds during 1–11 April inclusive, in all three years all did so on the first tailwinds available after periods of headwinds in the middle of the month (Fig. 3).

### Migration routes

Geese flew direct from Ireland to Iceland, although one bird showed very slow progress and may have stopped briefly in SW Scotland en route (Fig. 4). All migrated to Iceland between 16 and 19 April in the three years. Average migration period was 25 h ( $\pm 4.2 \text{ SE}$ ,  $n = 7$ ,

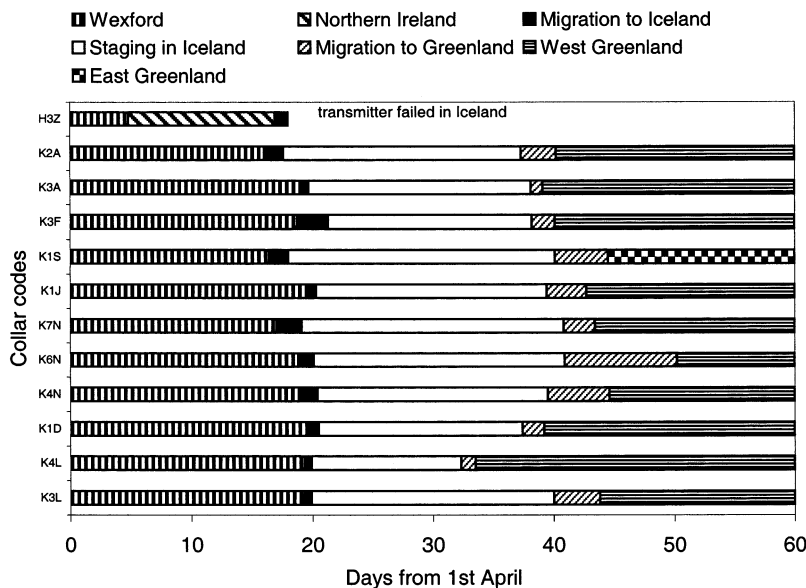


Fig. 2. Migration schedules of Greenland white-fronted geese, showing the timing of spring migration events of individuals marked with satellite transmitters. Codes (left) identify geese by the engraved codes on the collars they bore. Histogram columns indicate the duration of migration to Iceland, staging period there and migration to Greenland.

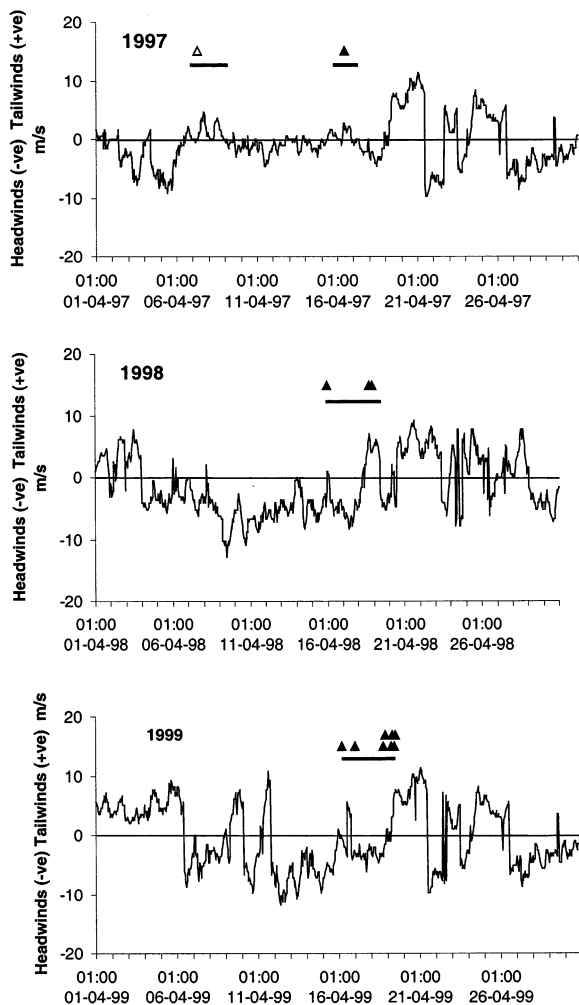


Fig. 3. Tailwind (positive) and headwind (negative) effects of prevailing wind conditions based on wind direction and speed at Kilkenny, 80 km WNW of Wexford throughout April 1997, 1998 and 1999. Wind vectors were calculated relative to observed tracks of geese followed by satellite telemetry following the methods of Piersma and Jukema (1990) calculating ground speed along the mean direction taken minus airspeed based on prevailing wind strength and direction, based on hourly observations. Triangles indicate the point of departure for satellite tagged geese to Iceland in the three years. The single bird with a functioning radio departed from Wexford 7 April (open triangle) and staged in northern Ireland (in association with other geese from Wexford) from whence it departed for Iceland on 16 April 1997. Solid horizontal lines indicate periods when there were large departures of geese reported from the site.

range 13–77). Four geese appeared to overshoot and return to western Iceland in 1999 (Fig. 4). All did so during the period 10:10 pm on 19 April to 06:30 am the next day, when E-ESE winds of ca  $74 \text{ km h}^{-1}$  (Danish Meteorological Institute data) prevailed off SW Iceland. The resulting ground speed of a goose flying  $60 \text{ km h}^{-1}$  could approach  $95\text{--}130 \text{ km h}^{-1}$  in such strong following/side wind conditions. Transmitters on two of

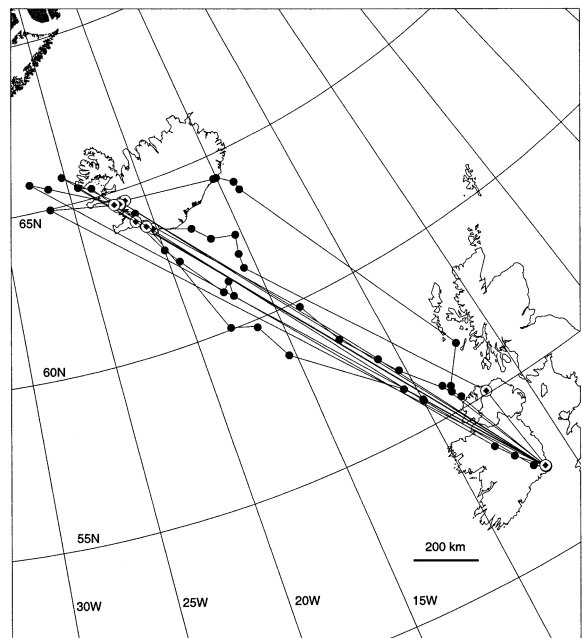


Fig. 4. Spring migration routes taken by 12 Greenland white-fronted geese fitted with satellite transmitters at Wexford, SE Ireland, to staging areas in SW and W Iceland during 1997–1999. Large black-centred dots: staging areas used for more than 2 days. Small black dots: up-link points during migration. Double stereographic projection generated in MapInfo, with lines indicating loxodromic distances between points.

these birds provided fixes that suggested repositioning return flights, and all four individuals subsequently staged in Iceland for normal periods before migrating onwards to Greenland. Transmitters on two other geese migrating at the same time provided no positional data during this period and the remaining geese undertook their migration flights under different wind conditions.

### Staging period in Iceland

It was not possible to precisely determine the staging times of all geese staging in Iceland. For H3Z, the transmitter failed during the staging period, and for three other birds, the duty cycle rest period obscured the precise departure time. For those individuals where arrival and departure time can be estimated with  $< 12$  hours accuracy, the mean staging period was 18.5 days ( $\pm 1$  SE,  $n = 11$ , range 12.5–21.8). One bird, K1S, spent 5–7 days in the southern lowlands before moving to the west coast for a further 14–16 days.

### Body condition prelude to departure, Hvanneyri

Based on mean scores of abdominal profiles, there was little difference between the rate of body mass accumulation in all three springs (Fig. 1). Low temperatures

during 4–10 May 1997 and 1999 (based on daily mean minimum temperatures at Stykkisholmur 65° 05'N 22° 44'W from the Icelandic Meteorological Office) apparently adversely affected the late accumulation of body stores in those years (Fig. 1). There was also very good correspondence between increase in total body mass and abdominal profile score as discussed elsewhere (Fig. 1, Nyegaard 2001, Fox 2002).

### Departure times from Iceland

Departure times and passage duration are shown in Fig. 2 and 5. In 1997, none of the satellite transmitters continued to function beyond Iceland, but observations of departing geese were made on the ground in all three

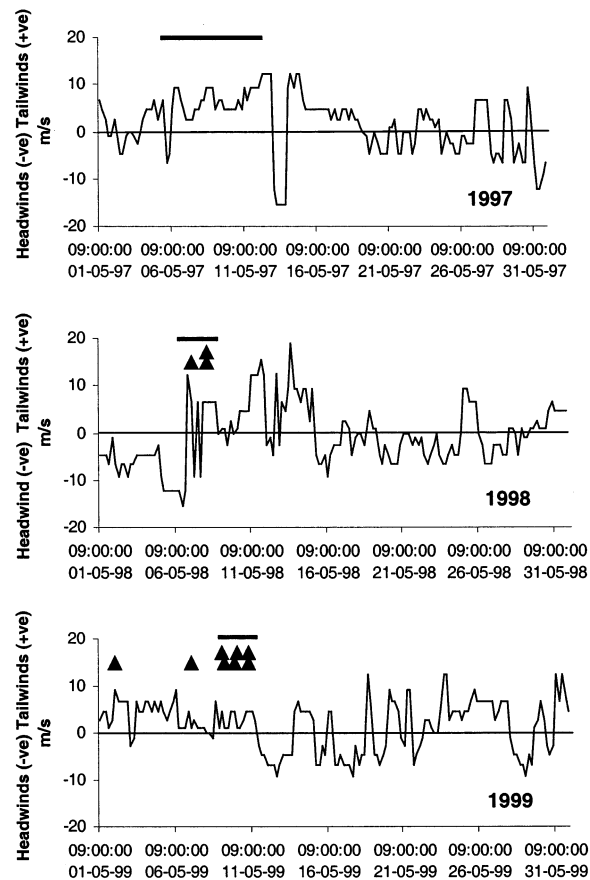


Fig. 5. Tailwind (positive) and headwind (negative) effects of prevailing wind conditions based on wind direction and speed at Stafholtsey, 10 km NE of Hvanneyri throughout April 1997, 1998 and 1999. Wind vectors were calculated relative to observed tracks of geese followed by satellite telemetry following the methods of Piersma and Jukema (1990) calculating ground speed along the mean direction taken minus airspeed based on prevailing wind strength and direction, based on hourly observations. Triangles indicate the point of departure for satellite tagged geese to Greenland in the three years. Solid horizontal lines indicate periods when the last 50% of peak numbers of geese left the site (see Fig. 4 in Fox et al. 1999).

years at Hvanneyri. Geese departed from Hvanneyri on favourable tailwinds and in 1999, two satellite tagged individuals departed with favourable tailwinds prior to the major departure and that of the remaining tagged individuals (Fig. 5).

### Migration routes

Geese completed the journey from Iceland to West Greenland in very different times. At least 4 individuals in two years appeared to stage on the edge of the sea ice ca 30 km from the East Greenland coast for a minimum of three to seven hours (Fig. 2 and 6). Three birds stopped on the East Greenland coast for between one and 20 hours, while one bird began the traverse of the ice cap, turned back and summered in east Greenland. Several individuals made slow progress crossing the Greenland ice cap, all flying in the direction of their ultimate destination (i.e. not necessarily taking the lowest or shortest crossing routes). A full analysis of these observations will be published elsewhere, but average journey time from Iceland to west Greenland (ca 1400 km) was 82 h ( $\pm 20.9$  SE,  $n = 10$ , range 24–261), with three birds potentially making the journey in less than 36 hours.



Fig. 6. Spring migration routes taken by 11 Greenland white-fronted geese fitted with small satellite transmitters at Wexford SE Ireland, from SW and W Iceland to West Greenland during 1998 and 1999. Signals from a twelfth goose stopped on the staging area in Iceland. Large black-centred dots: staging areas used for more than 2 days. Small black dots: up-link points during migration. Double stereographic projection generated in MapInfo, with lines indicating loxodromic distances between points.

## Discussion

### The effects of transmitters

It seems unlikely that birds carrying transmitters such as these are likely to behave normally. Externally mounted equipment on a flying bird must affect their drag characteristics and hence flight performance, even allowing for the fact that birds could be seen to preen the transmitters under the feathers. We can only speculate on what effect this had on the individuals concerned, but for the purposes of this analysis, we assume the transmitters had no major effect on goose behaviour. The timing of migration of tagged birds coincided closely with the observed departures from Ireland and Iceland. The arrival in Greenland of the first tagged goose, K4L, coincided with the normal first arrival dates there, and most of the birds arrived at the time of peak numbers at spring staging areas (i.e. 9–15 May, Fox and Madsen 1981, Fox et al. 1983, Glahder 1999a). The routes they took were not unusual. All birds carrying functional transmitters reached their summer range, with the notable exception of the one bird that returned and remained on the east coast of Greenland after apparently attempting to traverse the Greenland ice cap. This bird returned safely to the wintering grounds in the subsequent season. There were no signs of behavioural costs to fitting of transmitters: twelve of the males were captured with mates and goslings, and in all cases where these individuals returned to the wintering area, all were still associated with surviving family members for the remainder of the time they were observed. The annual survival of the marked birds during the first four seasons after fitting of the PTTs was 76.1%, based on intensive observations of return rates to the wintering grounds. This falls on the 95% confidence intervals (mean 78.5%, 95% C.I. 76.2–80.5%) of the estimated annual adult survival based on capture-mark-recapture of 1255 Greenland white-fronted geese individually marked at Wexford during 1983–1997 (Fox 2002). None of the marked individuals have bred successfully (i.e. returned to the winter quarters with young) in the years following marking, but this is not unusual, given the unusually low recruitment rate amongst geese in this population (generally less than 10% of all marked gosling cohorts ever survive to breed, Fox 2002).

### Timing of departures from Ireland

Most long-distance migratory birds show dynamic pre-programmed changes to body condition (such as fat accumulation) with which to confront ecological barriers to be overcome by long distant flight (Alerstam and Lindström 1990, Berthold 1993). The timing of the onset of the return to the breeding areas is often under

endogenous control (Gwinner 1986, 1987, Piersma et al. 1990). However, the precise departure times of migrating geese are likely to represent a trade-off between many conflicting factors. Perhaps paramount is the internal condition of the individual – threshold stores of fuel and appropriate flight musculature must be attained before undertaking a flight across the sea to Iceland that offers no refuelling opportunities en route. Although one goose in 1997 chose to stage within Ireland before departing for Iceland, it did so early on, hence we are confident that most of the tagged individuals made the flight across the sea in a single flight (Fig. 4). The increasing rate of body accumulation evident from the weights of caught birds through the latter part of the winter suggests that there is a rapid hyperphagia immediately prior to departure. Each extra day represents the accumulation of more mass than the previous daily increment in anticipation of the demands on stores made by the migration episode (Fig. 1). Therefore to leave in the first ten days of April is to potentially sacrifice a period of rapid accumulation of body mass on the wintering grounds. Furthermore, despite the rapid increase in solar insolation throughout the month of April, mean daily minimum air temperatures on Icelandic staging areas remain below freezing until 25 April. In Iceland, geese feed on hayfield grasses during the earliest stages of growth (Fox et al. 1998c, Kristiansen et al. 1998, 2000) and on wetlands, exploiting sub-terranean over-wintering organs of *Carex lyngbyei* and *Eriophorum angustifolium*, before their onset of growth (Francis and Fox 1987, Fox et al. 1999). In normal seasons, the ground temperatures in the first 10 days of April are unlikely to be conducive to either grass growth or deep melting of the substrate (to enable uprooting and extraction of sedge lower stems). Hence, the natural variation in food availability in Iceland is likely to favour geese remaining on the wintering grounds until the middle of April.

The continued increase in API scores throughout the month of April suggests that there is no cost (in terms of stabilising or reduction in body mass) to remaining at Wexford late into month. This is despite the falling numbers observed in the latter half of the month, when it might be expected that the remaining sampled birds were those in poorer condition than those that had already left, hence reducing the mean API score at this time. Although we have no nutritional analysis to confirm this, it would appear geese can remain as late into April as need be, given that there is no evidence to suggest they cannot sustain increasing rates of body mass to the end of that month.

However, there could be an upper threshold level of body mass above which flight become less efficient or where predation risk becomes a factor in defence of body stores. Given the continued increase in API throughout April, this seems unlikely, but could be a contributory factor to deciding when to leave.

During the 3 years of the study, geese waited until mid April before departing Ireland. Tagged individuals departures corresponded with onset of tailwinds (after prolonged periods of headwinds) to assist flight. They did not take advantage of tailwinds in early April, although one bird did so to fly to Northern Ireland to complete pre-migration fattening without departing to Iceland at that time. Very few mass departures occur from Wexford before ca 17 April, despite suitable wind conditions (AJW personal observations). Presumably increases in body mass attainable at Wexford and the uncertainty of conditions in Iceland mitigate against departure before that time.

### Timing of departures from Iceland

Geese face a similar trade-off in Iceland, balancing the accumulation of sufficient stores to make the flight to ensure arrival times that, for a breeder, offers best potential to raise most young successfully, against the risk of encounter of severe weather en route and on arrival. In particular, the severe conditions on the mountains of East Coast of Greenland and the clearance of the inland Ice cap are known to present particular challenges to migrating geese (Guðmundsson et al. 1995). Despite considerable differences in temperature in particular, and weather patterns in general between the springs of 1997, 1998 and 1999, the relative rate of increase in average abdominal profile scores of geese was remarkably similar in all three years (Fig. 1). This may be because the use of API scores represents a crude measure of general changes in body mass that are mainly (but not exclusively) to do with changes in the extent of fat deposits concentrated in the abdomen. However, there is a good predictive relationship between API score and body mass that is consistent between different seasons (Fox 2002, unpubl.). Although we need more catches in more seasons of greater samples of birds to confirm the general similarity in mass accumulation in Iceland in spring, the implication is that birds are able to accumulate increasing body mass in a fairly predictable linear pattern at this time. This is slightly different to the case in Ireland, where to remain longer results in increasing daily mass increment as the season progresses, but again implies no obvious cost to remaining on staging areas in Iceland into May. In Greenland, on arrival, geese fed on subterranean overwintering storage organs of plants, primarily the lower stem *Eriophorum angustifolium* in organic substrates, and the rhizomes of *Puccinellia deschampsoides* and bulbils of *Triglochin palustris* extracted from more mineral soils in wetlands at low altitude (Fox and Madsen 1981, Madsen and Fox 1981). This necessitates thawing of upper horizons of the substrate to permit extraction of these plant parts, since there is no above ground production of green

plant parts in early May in West Greenland. This in turn requires daily maximum temperatures above 0°C, even though feeding is modified and finally ceases at night when substrates are frozen (Fox and Madsen 1981). For breeding females, it seems likely that there is a period of rapid follicular development that occurs after arrival on the summering areas, thought to last 7–10 days in white-fronted geese (Ely and Raveling 1984). There is therefore generally a period of 2–3 weeks between peak arrival time and first egg dates amongst Greenland white-fronted geese during which time, the females feed intensively on plant storage organs, protected by attendant ganders (Fox and Madsen 1981, Fox et al. 1983, Glahder 1999a). For these birds, the advantage is to be first, and to be first in best body condition, since in all studies of northern nesting geese, earliest breeding birds produce the greatest numbers of young (Cooke et al. 1995, Kokko 1999). To arrive in west Greenland too early or to inclement weather, such as deep snow (i.e. to inaccessible food resources) risks consumption of remaining stores not exhausted in the strenuous flight to the summering grounds. Arriving late carries no direct costs except for local food depletion as a result of intra-specific competition, but the physiological limit of follicle development means delay to first egg dates and the costs in terms of reproductive output that this incurs. Goose migration is generally delayed in years when headwinds prevail (Ebbinge 1989, Green 1998), suggesting a general avoidance of the energetic flight costs of setting off into a headwind versus a tailwind (Butler et al. 1997). Hence, we would again expect the birds to have an optimal departure date from Iceland, which is perhaps largely under endogenous control, but that individual departure dates represent a trade-off between internal state and availability of favourable winds about that time. This appears to be the case, such that after geese had recouped 300–400 g of body mass between 20 April and 5 May (Fig. 1), the actual departure dates appeared to be influenced by availability of favourable winds in the springs of 1997–1999. Unfortunately, there are no data on departure dates from other years in Iceland. Regular census in southern Iceland in 1990–1992 suggested most staging birds there were gone by 8 May, and there is a very rapid reduction in reports of collared birds from Iceland after 7 May (Fox et al. 1999).

### Attempting to understand the trade-off between body condition and optimal departure time

Tagged geese certainly appeared to wait for tailwinds to start out on their migration journeys across the sea from Ireland and from Iceland, but we lack sufficient data to confirm a link between migratory departure decisions and the strength and availability of assisting



tail winds. In particular, we lacked frequent API determinations from satellite tagged geese to establish links at the individual level. We shall explore the energetic consequences of such a decision in a future analysis, but some geese departed on suitable winds earlier than others, why should this be? It seems likely that this could be the result of body condition. If we use API as an index of condition, and use the mean rates of increase derived from observations in Fig. 1, we can conceptualise the changes in body condition through migration from Ireland to Greenland as shown in Fig. 7. For simplicity, we make the assumption that the very fittest birds arrive earliest after 1 May (when the first birds usually arrive in Greenland, Fox et al. 1983) and hence breed first and are most successful (although this depends on conditions on arrival). We also make the simple assumption that an API of 3.2 represents a threshold fat accumulation that will enable to flights from Ireland to Iceland and Iceland to Greenland and enables an attempt at reproduction. In Fig. 7, the thin lines represent the average goose A based on multiple observations, the thicker line an individual B that is more efficient at accumulating stores. B attains fat deposits sufficient to depart on 16 April, compared to 6 days later for A. Assuming suitable tail winds prevail, B can make the crossing to Iceland before the bird show-

ing average condition. Even if suitable winds are not available until 22 April, when the A has stores enough to depart, B departs in favourable winds with greater stores, and assuming the flight costs are the same, arrives in slightly better condition than A (although the extra body weight could reduce flight performance). Assuming similar rates of fat deposition in Iceland, regardless of timing, B retains this advantage, even if constrained to depart with A on the same winds, in this case resulting in attaining stores for reproduction two days earlier than A (Fig. 7). In fact, an efficient forager may accumulate stores faster in Iceland and Greenland and therefore increase its advantage over the average bird. This type of approach is highly speculative, but is useful in showing how small differences in foraging efficiency and the interplay between internal body condition and external wind conditions interact to underpin departure decision-making for spring migrating geese along their flyway.

We are still a long way from understanding how geese decide to start on a migration episode, not least because we have here only considered ground wind conditions, and have yet to demonstrate that these geese migrate at low altitude. In the present analysis, we have not considered other meteorological cues to trigger onset of migration, such as temperature, nor

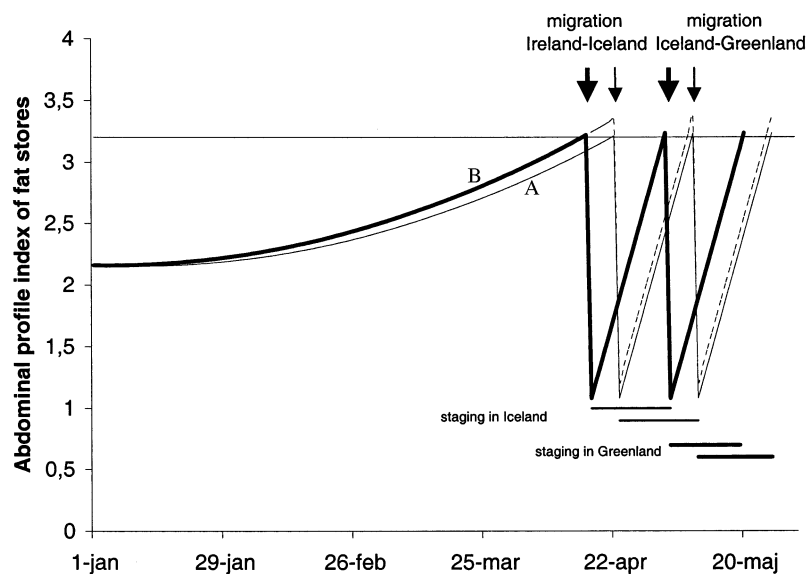


Fig. 7. Schematic diagram illustrating the potential changes in abdominal profile (API) scores as an index of body stores of two Greenland white-fronted geese, a bird that follows the average rate of fat deposition (A, the thin line) and one that accumulates fat stores more rapidly (B, thick line). Assuming threshold stores at API 3.2 (thin horizontal line) will sustain migration to Iceland and Greenland and enable a reproductive attempt, goose B will be ready to depart the wintering grounds 6 days before goose A, and therefore will have potentially more days when tailwinds could assist passage to begin migration. In this case, arriving earlier in Iceland, B will be able to take advantage of tailwinds by 3 May to continue to Greenland and be in condition to breed by 20 May. Even if tailwinds do not occur until goose A has attained sufficient stores, B still arrives in Iceland with greater stores remaining (assuming costs are the same to both individuals, see thin peaked line). Assuming similar rates of accumulation in Iceland, and synchronous departure on 10 May, goose B still attains breeding condition by 25 May, two days before A. Given identical costs, but asynchrony in foraging efficiency in Iceland and Greenland, it is likely B will further gain extra store deposits in advance of A along the route.

how conditions at the point of departure reflect wind (or other conditions) encountered along the entire route (Green et al. 2003). Geese migrate in social units and decisions to depart a staging area involve at least two individuals of a pair and usually more members of a family unit. However, the results of this investigation suggest the interaction between internal (body conditions) and external (wind strength and direction) in departure decision-making to ensure safe arrival at summering areas by optimal time.

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